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Mirounga leonina. By J. K. Ling and M. M. Bryden

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***Mirounga* Gray, 1827**

Macrorhinus Gray, 1825:340. No species mentioned; preoccupied by *Macrorhinus* Latreille, 1825, a genus of Coleoptera.

Macrorhinus E. Geoffroy St.-Hilaire and F. Cuvier, 1826:552. Type species *Phoca proboscidea* Péron, 1816, by original designation; = *Phoca leonina* Linnaeus, 1758. Junior homonym of *Macrorhinus* Gray, 1825, and of *Macrorhinus* Latreille, 1825.

Mirounga Gray, 1827:179 (part, described as a subgenus of *Phoca*). Type species *M. proboscidea* (Péron, 1816) by subsequent designation (J. A. Allen, 1905:94); = *Phoca leonina* Linnaeus, 1758.

Macrorhyna Gray, 1827:180; incorrect subsequent spelling of *Macrorhinus* E. Geoffroy St.-Hilaire and F. Cuvier, 1826.

Rhinophoca Wagler, 1830:27. Replacement name for *Macrorhinus* E. Geoffroy St.-Hilaire and F. Cuvier, 1826.

Cystophora Nilsson, 1837:250 (part, not *Cystophora* Nilsson, 1820).

Morunga Gray, 1837:582. Incorrect subsequent spelling of *Mirounga* Gray, 1827.

Physorhinus Gloger, 1841:163. Type species *Physorhinus proboscideus* Gloger, 1841, by monotypy; preoccupied by *Physorhinus* Eschscholtz, 1836, a genus of Coleoptera.

CONTEXT AND CONTENT. Order Carnivora, Superfamily Phocoidea, Family Phocidae, Subfamily Monachinae, Tribe Lobodontini. The genus contains two species. A key to the species based on Briggs and Morejohn (1976) and King (1983) follows:

- 1 Proboscis not pendulous and does not hang beyond mouth; skull foreshortened; lower post-canines tend not to be multicused and multirooted; often assumes U-shaped posture; restricted to Southern Hemisphere *M. leonina*
- 2 Proboscis pendulous and overhangs mouth; skull elongated; lower post-canines tend to be multicused and multirooted; seldom assumes U-shaped posture; restricted to Northern Hemisphere *M. angustirostris*

***Mirounga leonina* (Linnaeus, 1758)**

Southern Elephant Seal

[*Phoca*] *leonina* Linnaeus, 1758:37. Type locality "ad polum Antarcticum"; restricted to Juan Fernandez Islands by Thomas (1911:133); further restricted to Isla Mas a Tierra, Islas Juan Fernandez, Chile, by Scheffer (1958:129).

Phoca elephantina Molina, 1782:280. New name for *Phoca leonina* Linnaeus, 1758.

Phoca proboscidea Péron, 1816:34. Type locality "des regions Australes" (p. 37).

Phoca resima Péron, 1816:66. Type locality "des iles St.-Pierre et St.-Paul d'Amsterdam."

Phoca coxii Desmarest, 1817:559. Type locality "les iles de Saint-Paul et d'Amsterdam," Indian Ocean.

Phoca ansonii Desmarest, 1820:239. Type locality "L'île Georgia, la Terre de Feu, les îles Malouines, la côte est de l'Amérique, depuis la Terre des Etats jusqu'à 40°. degré, sur la Terre des Patagons; quelques îles Sainte-Hélène, selon Dampier, la Terre de Kerguelen?"

Phoca ansonina De Blainville, 1820:299. Type locality "des îles Felckland [sic]."

P[hoca]. *ansonii* De Blainville, 1820:300, alternate spelling of *Phoca ansonina*.

Macrorhinus proboscideus: E. Geoffroy St.-Hilaire and F. Cuvier, 1826:552, name combination.

Macrorhinus ansonii: Lesson, 1827:202, name combination.

[*Phoca*] *M[irounga]. proboscidea*: Gray, 1827:180, name combination.

[*Phoca*] *M[irounga]. proboscidea*: Gray, 1827:180. Based on

"Phoque des Patagons" (F. Cuvier, 1824:pl. 14, fig. 2) from "la côte des Patagons" (p. 203).

[*Phoca*] *M[irounga]. ansonii*: Gray, 1827:180, name combination. *Ph[oca]. dubia* Fischer, 1829:235. Type locality "In insulis Malvinis."

Cystophora proboscidea: Nilsson, 1837:240, name combination.

Macrorhinus coxii: Boitard, 1842:277, name combination.

Morunga elephantina: Gray, 1844:4, name combination.

[*Cystophora*]. *salklandica* Peters, 1875:394 (footnote). Based on Pernety (1769); therefore, type locality Falkland Islands.

[*Cystophora*] *kerguelensis* Peters, 1875:394 (footnote). Type locality "kerguelenland."

Cystophora elephantina: Brehm, 1877:638, fig., name combination.

Macrorhinus leoninus: J. A. Allen, 1880:456, name combination.

Mirounga leonina: J. A. Allen, 1905:95, first use of current name combination.

CONTEXT AND CONTENT. Context noted in generic summary above. Lydekker (1909) proposed three subspecies of uncertain validity (Scheffer, 1958):

M. l. crosetensis Lydekker, 1909:606. Type locality "Crozet Islands."

M. l. falcandicus (Peters, 1875:394), see above.

M. l. macquariensis Lydekker, 1909:603. Type locality "Maquarie [sic] Islands."

However, Bryden (1968a) regards the different growth patterns of populations on Macquarie Island and in the Falkland Islands Dependencies as being phenotypically determined and not indicative of subspecific rank.

DIAGNOSIS. *Mirounga* is distinguished from other pinnipeds by the giant size of adult males (mass >3,000 kg and >6 m in length) and their pendulous, elephantine proboscis (Fig. 1). *M. angustirostris* inhabits the Northern Hemisphere and *M. leonina* the Southern.

GENERAL CHARACTERS. Diagnostic features of the skull (Figs. 2, 3) are related to the inflatable proboscis that is most pronounced in adult males. The mean basilar length is 64% greater in males (453 mm) than females (277 mm); the palatal length 79% greater (283 and 133 mm); and zygomatic width 57% greater (332 and 211 mm; Briggs and Morejohn, 1976). After each annual molt,



FIG. 1. Photograph of *Mirounga leonina* showing adult male (beachmaster) and female at Macquarie Island. Note the sexual dimorphism between the larger male and smaller female; and also the human figure for scale. Photograph by J. Bray.

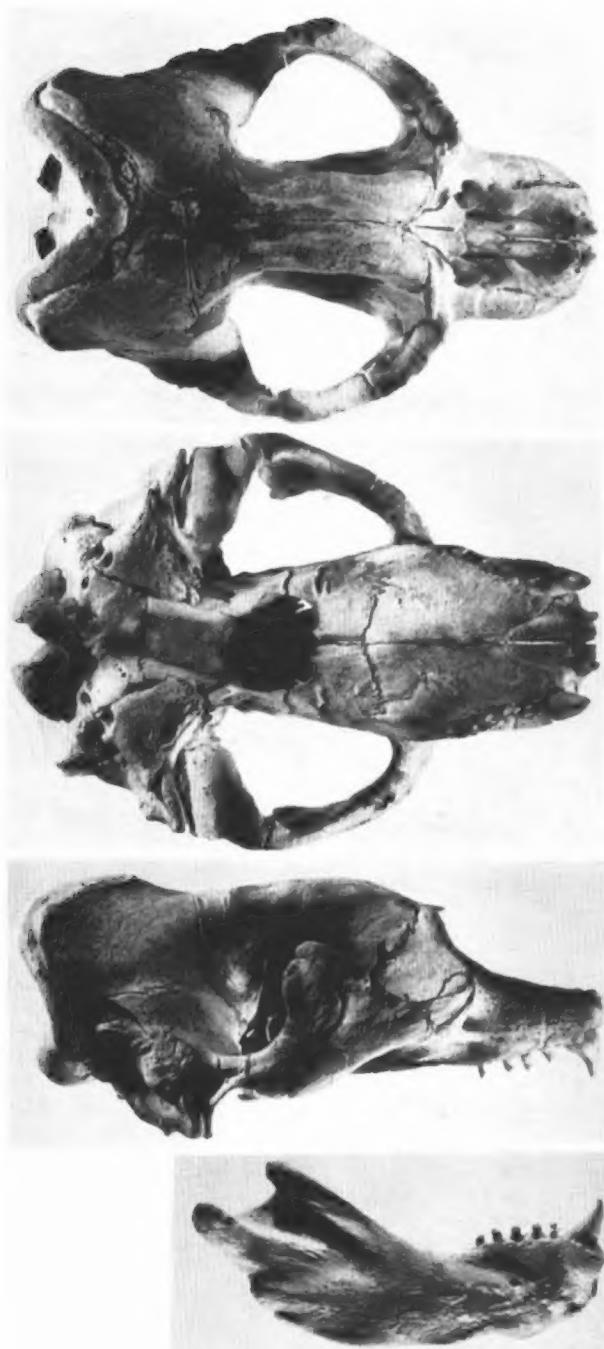


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of a male *Mirounga leonina* (South Australian Museum M3744 from Adelie Land, Antarctica). Condyllobasal length of cranium is 324.0 mm.

adult southern elephant seals range in color from a dark slate-gray to brown, somewhat lighter ventrally. Males are larger than females, the maximum recorded standard lengths being 620 and 368 cm, respectively, at Signy Island (Laws, 1953a) and 467 and 250 cm, respectively, at Macquarie Island (Ling and Bryden, 1981). Elephant seals grow faster, mature earlier, and die younger than phocines (Laws, 1959). Milk dentition is i 2/1, c 1/1, p 3/3, total 22, and adult dentition is i 2/1, c 1/1, p 4/4, m 1/1, total 30.

DISTRIBUTION. The species has a circumpolar range (Carrick and Ingham, 1962a; Scheffer, 1958), but populations are concentrated on and around sub-Antarctic islands lying near the Antarctic Convergence (Fig. 2). Elephant seals regularly haul out in Antarctica near the Vestfold Hills (Gales and Burton, 1989) and

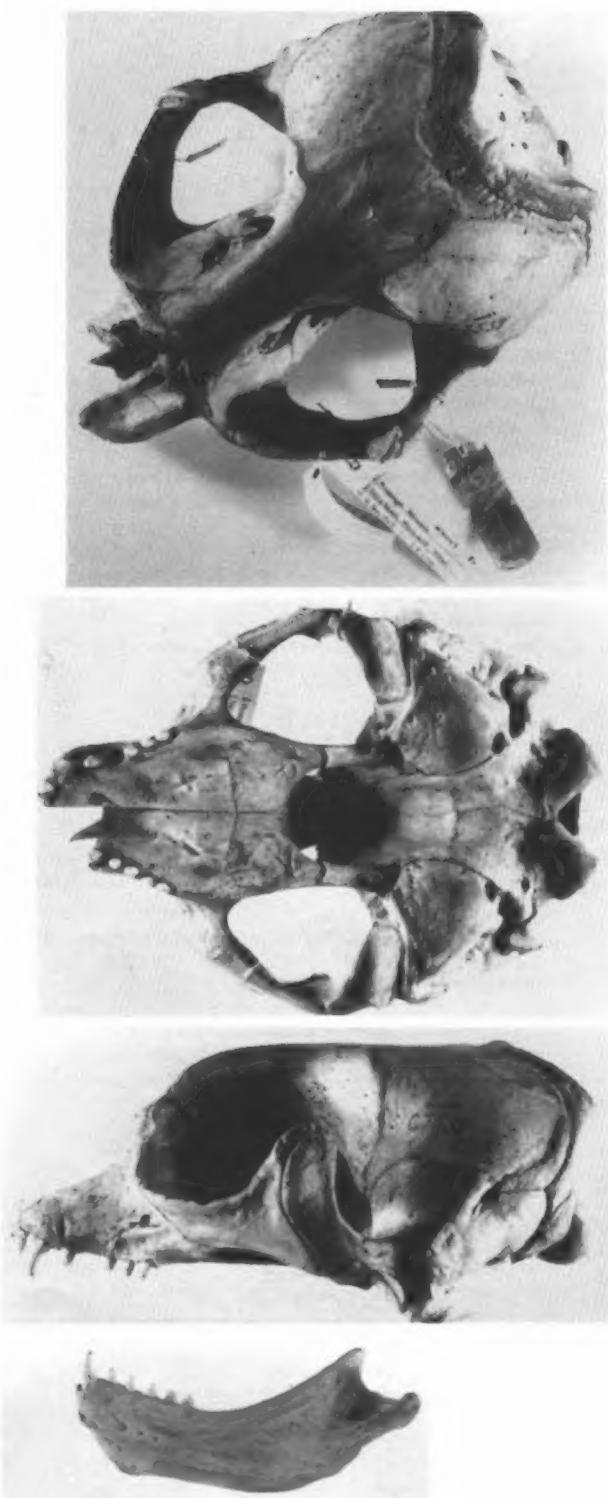


FIG. 3. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of female *Mirounga leonina* (South Australian Museum M14447 from Macquarie Island). Condyllobasal length of cranium is 285.0 mm.

births have been recorded in Antarctica (Murray, 1981); they once bred on the northwestern coast of Tasmania and on King Island in Bass Strait (Australia) where they are now extinct. Occasional births have been reported from New Zealand (Bowring and Stonehouse, 1968), South Africa (Kettlewell and Rand, 1955), and Australia (Robinson and Dennis, 1988; Tyson, 1977). The northernmost record for the species is from Saint Helena (16°S; Fraser, 1935). Laws

(1960) estimated the world population of southern elephant seals as almost 600,000 in mid-year. McCann (1985) amended this figure to 750,000 with the main populations at South Georgia (350,000), Iles Kerguelen (157,000), Heard Island (80,000), and Macquarie Island (136,000). There is growing evidence, however, that some island populations in the southern Indian and southern Pacific oceans are declining (Burton, 1986; Condy, 1984; Hindell and Burton, 1987).

FOSSIL RECORD. Fossils of the genus are unknown, but the ancestor of *Mirounga* was probably of the same stock as *Monachus*. *M. leonina* must have been derived from some of these stocks that moved south along the Pacific coast of South America in the Pliocene (King, 1983).

FORM. The pups are born with a long, dark, brownish-black, curly fur that is replaced by the first, shorter, adult-type pelage at about 3–4 weeks of age (Ling and Thomas, 1967). Young seals have a silvery-gray dorsal and lateral pelage and a creamy venter, but the pelage darkens with age. It also becomes dirty and stained by feces, mud, and urine in wallows; only freshly molted seals present a true color. Some old seals fade to a pale creamy-white hue. There is no underfur. The hair follicles are simple and unbranched and produce single, stiff, lanceolate hairs 10–15 mm long, flattened at right angles to the long body axis and sloping backwards. Older seals have dry, scaly, and cracked skin that often is scarred from wounds (Ling, 1968). The hairs are attached by their roots to the epidermis (Ling and Thomas, 1967) and are shed annually in large sheets, according to a definite topographic sequence during the austral summer months. The timing of the molt is closely related to age and reproductive status. It is quickest in females that pupped during the previous breeding season that molt in deep, warm, muddy wallows where increased skin temperatures may accelerate epidermal cellular activity (Ling and Bryden, 1981). Adult males molt in shallower wallows or mud pools, and immature seals of both sexes molt on the beach and among tussock grass (*Poa foliosa*) just above the beach. Immature seals molt in November or December, followed by primiparous females, then older females in January and February and, last, mature males from February to March or even later (Ling, 1965; Ling and Bryden, 1981).

The epidermal thickness varies from 150 to 500 µm, depending mainly on the depth of the horny layer; and the combined thickness of epidermis and dermis may reach 5 cm in the heavily bosselated throat region of adult males. The depth of subcutaneous blubber varies from 5 to 15 cm in different body regions, depending on the age and sex of the seals and the season (Ling, 1968).

There are three groups of facial vibrissae: mystacial, suprabital, and rhinal containing approximately 38, 7, and 1 hairs, respectively (Ling, 1966). The mammae are usually two, but sometimes three or four in number (Laws, 1956a). There are striking changes in milk composition at different stages of lactation during the cycle, particularly at 7–14 days. Fat and protein contents are high; carbohydrates negligible. The rate of milk production also changes with time, ranging from 100 ml/12 h at birth to 650 ml/12 h at 7 days and 300–600 ml/12 h at 14 days (Bryden, 1968b). The milk teeth are resorbed during the second one-half of the gestation period and permanent teeth begin to erupt at about the time of birth. All teeth have erupted about 35 days after the pups are weaned (Ling and Bryden, 1981). Distinct growth layers develop in the teeth and are useful for age determination (Carrick and Ingham, 1962b).

The skeleton, apart from the skull (Figs. 2, 3), is similar to that in other Phocidae. King (1972) observed modifications in the skull related to the possession of a proboscis that acts as a resonating chamber. In males, the skull continues to grow until at least 11 years of age; the snout grows faster than other facial regions, which grow faster than the cranium. The vertebral formula is typical for phocids: C7, T15, L5, S3, Cd11; although in 5–10% there are 14 thoracic and 6 lumbar vertebrae (Ling and Bryden, 1981). The musculature is associated with the greater terrestrial activity of *Mirounga* than some other phocids and shows some similarities to that of otariids (Bryden, 1971a, 1973).

The venous system is similar to other phocids (Harrison and Tomlinson, 1956). The spleen is large as in other pinnipeds; it is an elongated oval, smooth, unlobed organ (Blessing et al., 1972). At birth, the brain mass is 540 g in males and 500 g in females, and in adults it is approximately 1,350 and 900 g, respectively, for males and females (Bryden, 1971b). The pineal gland of adults is

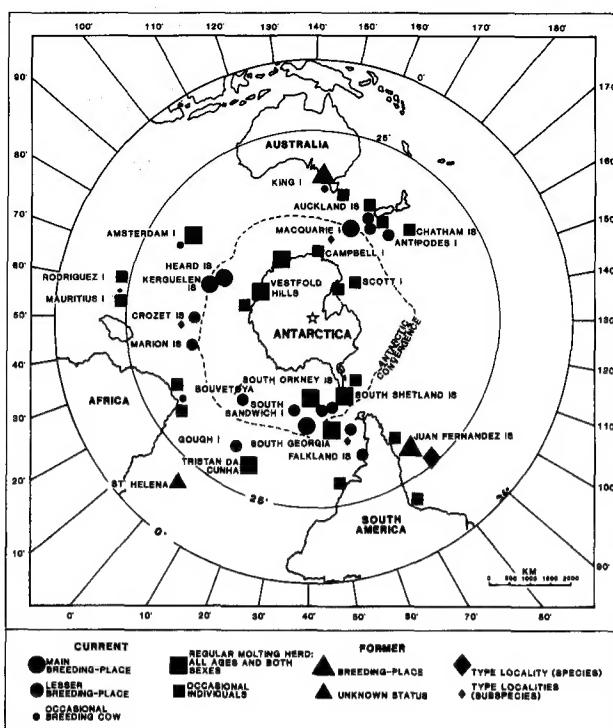


FIG. 4. Map showing past and present distribution of *Mirounga leonina*, and type localities of species and subspecies (modified from Carrick and Ingham, 1962a).

25–32 mm long, 5–9 mm wide, and 5–7 mm thick and features an inner medullary and an outer cortical zone. This zonation is not present in pups (Tedman, 1977). The pituitary conforms to the general mammalian pattern (Griffiths and Bryden, 1986).

The lungs comprise about 1.22% of total body mass in males and 1.34% in females (Bryden, 1971b). The stomach is simple and the small intestine exceptionally long (up to 202 m) with a narrow lumen and virtually no cecum (Laws, 1953a). The kidneys have five to eight lobes and are reniculate as in other seals (Arvy and Hidden, 1973; Harrison and Tomlinson, 1956). The testes lie outside the abdominal cavity in inguinal pouches beneath the blubber, where the testicular temperature varies from 30.1 to 30.6°C compared with 36.0 to 36.5°C body temperature (Bryden, 1967). There is an os penis, which is approximately 10 cm long at birth, 23 cm at 4 years, and 31 cm at 5 years, and 34 cm at 8 years (Laws, 1953b).

FUNCTION. The blubber acts as an effective insulator (Bryden, 1964), and its composition is similar to that of other seals. Depot-fat metabolism is mainly confined to long-chain fatty acids (Winter and Nunn, 1953). Blood volume is approximately 15% of body mass and the blood oxygen capacity (40 volumes percent) is greater than for any other marine mammal (Bryden and Lim, 1969; Scholander, 1940).

On land, elephant seals hitch themselves along on the relatively short foreflippers and the belly. In the water, they swim by means of a powerful sculling action through lateral movements of the body and hind flippers; the foreflippers acting only to assist in maneuvering. Even young pups can swim, but they generally do not enter the water until after the postnatal molt, and it takes about 1 week for them to learn to swim efficiently. Swimming speed in adults may reach 20–24 km/h (Laws, 1956a). They are capable of deep (1,200 m) and protracted (2 h) dives (M. A. Hindell, pers. comm.).

The mass of the adenohypophysis is small in autumn and winter, but increases significantly during the spring breeding season and summer. Gonadotropes are more common in sexually active males than in quiescent ones. Lactotropes are more numerous in midsummer than in midwinter. The lactotrope cycle is related to photoperiod, but not to breeding. Pineal gland activity is a function of the seasonal change in daylength (Griffiths and Bryden, 1986). Pineal mass and midday plasma-melatonin levels are greatest in midwinter and lowest in midsummer. Midday plasma-melatonin levels are inversely cor-

related with daily photoperiod (Griffiths and Bryden, 1981). Pineal gland activity decreases pituitary gonadotrophic secretions that in turn cause inactivation of the testes (Griffiths, 1985).

ONTOGENY AND REPRODUCTION. The right ovary usually ovulates first and the ovaries function alternately thereafter. Impregnation takes place about 18 days post partum. A 16-week free blastocyst phase follows and parturition occurs about 32.5 weeks post-implantation. There is one pup/year in a high proportion of mature females, and usually one ovulation a season; but an early breeder that misses impregnation may ovulate again (Laws, 1956b). The development and function of each corpus luteum is typically mammalian and the corpus albicans resulting from a pregnancy persists at least to the following breeding season. Ovarian evidence and data from aged seals at Macquarie Island suggest females reach sexual maturity at 3 years of age or older (Carrick et al., 1962a). Laws (1956b) believed that females at South Georgia Island matured at about 24 months; but McCann (1981a) amended this to about 36 months. The testes of male southern elephant seals are quiescent from December to July and spermatogenesis occurs from August to November (Griffiths, 1985; Laws, 1956b). Males in the South Georgia Island population in the 1950s reached sexual maturity at around 47 months and retained potency up to at least 11 years of age (Laws, 1956b). The ages of 20 harem males in 1977 ranged from 8 to 16 years (McCann, 1981a). Most males at Macquarie Island reach puberty at 6 years, but may not attain breeding status until 12, 13, or 14 years (Carrick et al., 1962b; Jones, 1981). This delayed maturity is believed to be typical of an unexploited population, such as existed at Macquarie Island in the 1950s, in contrast to the situation at South Georgia Island where large males were culled until the early 1960s.

Stillbirths are rare, but females may abort. Parturition is remarkably synchronous throughout the range, 80% of births taking place within a 3-week period around mid-October of an 8-week breeding season from mid-September to mid-November (Carrick et al., 1962b; Rothery and McCann, 1987). Pups are born either head-first or tail-first, with the latter being slightly more common. Twins are rare (Carrick et al., 1962a). Males tend to be heavier than females at birth. Birth mass is greater, gain in mass is faster, and molting is delayed at colder, more southerly islands (Condy, 1980). Newborn pups at Macquarie Island weigh approximately 38 kg and are about 127 cm from nose to tail. They are lighter, but not shorter than pups at Signy Island in the South Orkneys (Carrick et al., 1962a; Laws, 1953a). Pups more than double their birth mass by the time they are weaned at 22–23 days (Carrick et al., 1962a; Condy, 1980; Laws, 1953a), when they are deserted by their mothers. Mortality in the first year is about 40% (McCann, 1985). Survival decreases after 11 years of age. Laws (1953a) found skeletons at Signy Island, aged 18 and 20 years, and Hindell and Little (1988) found branded males aged 17 years and branded females, aged 23 years and accompanied by pups, at Macquarie Island. Equations for the length/weight relationships for males and females, respectively, are: $W = 131.49 + 0.00002079L^3$ and $W = 195.51 + 0.00000400L^3$, where W is body mass in kg and L is the standard length in cm. The largest body mass for a male and female for which age, standard length, and body mass data are available are 191 months, 467 cm, 3,692 kg and 127 months, 250 cm, 359 kg, respectively (Ling and Bryden, 1981). Male and female southern elephant seals grow larger and more rapidly at South Georgia than at Macquarie Island (Bryden, 1968a).

ECOLOGY. Southern elephant seals normally inhabit beach and tussock areas on sub-Antarctic islands, but they may encounter ice and snow in the southernmost part of their range at Signy Island and on the Antarctic continent itself. Apart from man, killer whales (*Orcinus orca*) are their only predator, and inflict severe wounds on them. Many seals also become blind in one or both eyes (Carrick and Ingham, 1962c). Old males often carry goose barnacles (*Lepas*) attached to their skin (Carrick et al., 1962a). The louse *Lepidophthirus macrorhini* infests the hind flippers, particularly of pups (Murray and Nicholls, 1965). The acanthocephalan *Corynosoma bulbosum* has been described by Zdzitowiecki (1986) from the small and large intestine of *M. leonina*. Larvae of this parasite occur in the fish *Notothenia coriiceps* (Edmonds, 1957). The adult stage of *Porrocaecum decipiens* occurs in the southern elephant seal; *Notothenia* again being an intermediate host (Johnston and Mawson, 1943).

There is no interspecies competition and hardly any contact with other species. A male New Zealand sea lion (*Phocarcos hookeri*) was observed in the middle of a harem at Macquarie Island and to have attacked a pup (Csordas, 1963). At South Georgia Island, elephant seals are sometimes harassed by Antarctic fur seals (*Arc-tocephalus gazella*) occupying the same habitat, but the two species generally are separated in both space and time (Bonner, 1968). Elephant seals migrate from Macquarie Island to Campbell Island (Carrick et al., 1962b); and from Heard Island and Iles Kerguelen to Marion Island and the Vestfold Hills, Antarctica. Several hundred bachelor males haul out each summer to molt at the latter locality (Gales and Burton, 1989). Southern elephant seals tend to return to the same sites to breed each season, but disperse more widely at other times (Nicholls, 1970).

Underyearlings (<1 year old) undergo two distinct phases of movement at Marion Island: post-weaning phase that precedes departure from the island in January, involving only about 16.9% of this age class, and a resting phase when they return in March (Panagis, 1981). Weaned pups also disperse to other parts of Macquarie Island before leaving altogether; again hauling out to rest in March (Carrick et al., 1962a). However, at Iles Kerguelen, they mix randomly in well-defined dispersive areas by way of inshore waters, before becoming completely pelagic (Lenglart and Bester, 1982). Older seals move around islands during haul-out phases. Territorial behavior as such is not exhibited; harems of up to 1,000 breeding females are controlled by breeding males, the number of which varies according to the size of the harem. Many apparently suitable areas remain unoccupied by harems during the breeding season. Intraspecific competition for food, not space, was held to be the main population-regulating mechanism at Macquarie Island during the 1950s and 1960s, when the population was believed to be stable (Carrick et al., 1962a). Southern elephant seals have not been seen to drink actively, nor has feeding been observed or quantitative studies of diet carried out. Remains of fish (*Notothenia*) and cephalopods (*Gonatus antarcticus*, *Moroteuthis knipovitchi*, Octopoda, and unidentified teuthoids) have been found in stomachs (Clarke and MacLeod, 1982; Laws, 1956a).

Skinner and Van Aarde (1983) and Condy (1984) have documented an overall decline in the population of southern elephant seals at Marion Island between 1973 and 1983 of 8% for females and pups and 11% for males. Burton (1986) reported a 60% decline in pup production at Heard Island between 1949 and 1985 (31,827 and 13,111 pups, respectively). There has been an average annual decline of 2.1% in males and females at Macquarie Island between 1949 and 1985 for a 50% overall reduction (Hindell and Burton, 1987). Reasons for the declines are still obscure: predation by killer whales (*O. orca*), competition with man, or increasing numbers of fur seals on the feeding grounds (Condy 1978, 1981; Van Aarde, 1980a). Both Burton (1986) and Bester (1988a) suggest that food resources may be implicated in the decline of the Kerguelen stock of elephant seals, but McCann (1985) concluded that the fish populations could have been grossly underestimated, and hence declines in seal populations in the southern Indian Ocean should not be attributed to fishing operations. At South Georgia Island, the scene of intensive fishing effort, there appears to have been no decline (Rothery and McCann, 1987). At Iles Kerguelen, where there is evidence of a population slump since at least 1970, this may be part of a long-term, density-dependent fluctuation in the size of the breeding population. The degree of long-term fluctuations in numbers of females increases with density (Van Aarde, 1980a). Slight increases in female density on densely inhabited coastlines result in large increases in harem sizes and fewer harems (Van Aarde, 1980b). This correlates positively with the density of males in and around harems; numbers also correlate positively with numbers of females (Bester and Lenglart, 1982). The age structure of females at South Georgia Island has not changed since exploitation of males stopped in 1964, but changes were noted in time of male haul-out, number of males ashore, sex ratio, harem size, and the age of harem males. In addition, differences still persist between the South Georgia and Macquarie Island populations in respect to growth, body size, and population structure, due to differences in food availability at the two locations (McCann, 1980).

Southern elephant seals have been exploited in many parts of their range since the early nineteenth century, primarily for the oil produced from their blubber. This yielded from 1.5 to 2.5 barrels/seal from 1910 to 1958 when 259,026 males were killed at South Georgia Island (Laws, 1960).

Southern elephant seals have been shipped to zoos in Europe, North America, and Australia. The most successful zoo appears to have been at Stuttgart, West Germany, where elephant seals have survived for up to 22 years and four live pups were born. One pup lived for 14 months (Ling and Bryden, 1981).

In the course of long and short-term ecological and behavioral studies, southern elephant seals have been hot-iron branded, tagged, and paint-marked at the Falkland Island Dependencies (Dickinson, 1967; Laws, 1956a), Heard Island, Macquarie Island (Carrick and Ingham, 1962a; Ingham, 1967), Marion Island, and Iles Kerguelen (Van Aarde and Pascal, 1980). The drugs succinylcholine chloride, and ketamine in association with either diazepam or xylazine (Bester, 1988b; Gales and Burton, 1987; Ling et al., 1967; Ryding, 1982) have been used to facilitate a number of field studies requiring the application of invasive and non-invasive techniques such as blood and bacteriological sampling, skin biopsying, ultrasonic measurements of blubber thickness, and measuring and weighing larger animals. Smaller seals may be restrained manually using nets.

BEHAVIOR. Most behavioral observations have been carried out during terrestrial phases of the life cycle, but few have been made on southern elephant seals at sea, especially away from haul-out areas (McCann, 1981b, 1982, 1983; Van Aarde, 1980b). Terrestrial mating in this highly polygynous species is of crucial importance in the development and maintenance of a complex social organization, based on a dominance-hierarchical system, and timing of critical events in the annual cycle (Bartholomew, 1970; Carrick et al., 1962a; Laws, 1956a). Little change has occurred in the order or duration of haul-out pattern of breeding elephant seals over the last 35 years, and there is striking synchrony of timing of events in breeding females in populations of southern elephant seals (Hindell and Burton, 1988).

Breeding males arrive at rookeries first and patrol the beaches; followed up to 1 month later by gravid females, which select the most accessible areas along the beaches and aggregate spontaneously into groups of two to four to form the nuclei of harems. As more females arrive they are herded into harems by males whose main job then is to prevent females escaping before they are fertilized and also, insofar as the beachmaster is concerned, to ensure they are impregnated by no other males. Copulation frequency is related to male rank; top rank achieves 38% and the top five 82% of copulations. Status often is related to age and size (McCann, 1981b). Nearly all socially significant sounds are related to territorial invasion or defense and communication between females and pups on land. There is much less vocalizing in the non-breeding season when social relations are less complex (Laws, 1956a). Females emit a high-pitch moan or 'yodel' after the birth of their pup in response to the pup's sharp bark or yapping. Males emit a bubbling roar that appears to be produced in the throat as in a gargling action that results in a powerful, harsh, rattling sound capable of being heard (by humans) over many kilometers on a calm day. These roars come into play extensively in the establishment and maintenance of harems, and in over 90% of cases, suffice to win encounters; only 4% of which involve physical contact (McCann, 1981b).

Mean harem size at Iles Kerguelen (102–135) is greater than at South Georgia Island (64) where it varied from 41–124 females/harem (McCann, 1981a). However, on Macquarie Island, medium-sized harems contained 100–300 females and large harems 300–600 females; while one enormous harem held >1,000 females (Carrick et al., 1962a). Harems consisting of <50 females never contain more than one breeding male at a time. The number of breeding males varies from two or three in a harem of <100 females to about 30 in a harem of >1,000 females. Harem sites at Kerguelen ranged in order of use from sandy beaches to pebble beaches, vegetated hummocks, and cobble beaches (Van Aarde, 1980b). Substrate influences the size of harems, which coalesce on favored beaches if overcrowding occurs (Carrick and Ingham, 1960; Van Aarde, 1980b). Pup mortality tends to increase with harem size due to the confused activities of so many adult seals resulting in trampling of pups (Van Aarde, 1980b).

Females haul out about 1 weeks before giving birth, and suckle their pups for about 23 days (during which time impregnation occurs). After weaning, pups lie about in areas just above the beaches, molting and fasting for 3–7 weeks before going to sea and becoming nutritionally independent (Carrick et al., 1962a; Laws, 1956a). Virgin females are believed to be fertilized in the water, possibly by subordinate males (Laws, 1956a). Status of females is not necessarily

related to age or size, but young, small females tend to be of low status. High-ranking females rear larger pups that are attacked less frequently than pups of low-status females. Older females are more responsive to pup calls than younger ones (McCann, 1982). Both males and females spend most of their time ashore resting (and fasting), thus conserving energy. High-ranked males and pregnant females tend to be more alert, but the amount of time spent in agonistic activities is less related to rank. Male agonistic behavior is related more to the availability of females than the number of females ashore or the number of males in the female group (McCann, 1983).

Resting southern elephant seals disperse themselves in various attitudes and aggregations, apparently according to prevailing weather conditions. On heavily overcast, cold days, or with rain or snow blowing in a high wind, they lie packed closely together; whereas on warmer days with the sun out, they lie apart from each other, usually on their belly and often with sand tossed over their backs by a backwardly directed flick of the foreflippers (Laws, 1956a). They wriggle and jostle on another, scratch themselves a lot; and can reach all parts of their body with either the fore or hind flippers, the former having better developed claws than the latter. They do not groom each other and females do not clean newborn pups. Occasionally, a female will gently bite its pup; and irritable adult seals inflict much more aggressive bites on others of all ages and both sexes (Carrick et al., 1962a; Laws, 1956a).

Immature males indulge in play fighting, rearing up on their bellies and lunging at, but without wounding each other (Carrick et al., 1962a). Older males bite and tear each other's proboscis and neck, sometimes causing severe wounds and much blood to flow, but rarely resulting in death. Subordinate males tend to back off before coming into direct conflict (Carrick et al., 1962a; Laws, 1956a).

GENETICS. The diploid number of chromosomes for *M. leonina* is 34 (Årnason, 1974). Serologically, *Phoca*, *Erignathus*, *Mirounga angustirostris*, and *Leptonychotes* stand in a monophyletic unit relative to *Monachus* (Sarich, 1969). There is no hemoglobin polymorphism in *M. leonina* (Seal et al., 1971). No electrophoretic variation occurs in the blood proteins transferrin, haptoglobin, hemoglobin, lactate dehydrogenase, and caeruloplasmin in southern elephant seals from Macquarie Island (Shaughnessy, 1974). The Macquarie Island and Heard Island populations may have diverged genetically and only limited gene flow exists between the islands (Gales et al., 1989).

REMARKS. On the basis of comparison of their skulls, King (1966) placed *Mirounga* in the subfamily Monachinae. According to Strahan (1981) the generic name *Mirounga* was coined by Griffith et al. (in Gray, 1827) from an Australian Aboriginal dialect (*miou-round*) for elephant seal. The specific epithet *leonina* is derived from the Latin word *leoninus* meaning lion-like, but it is difficult to perceive any resemblance between a lion and an elephant seal, with its pendulous proboscis from which the vernacular name is derived.

Mirounga leonina is one of the most exhaustively and widely studied pinnipeds and its literature is correspondingly large. Ronald et al. (1976) and Kenny (1979) have compiled extensive bibliographies on *M. leonina*, including many older works.

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